On Limits to Seed Production

NOTES AND COMMENTS

ON LIMITS TO SEED PRODUCTION

The question is often posed whether seed production is limited by pollen supply or by resources available to the mother plant for maturing seeds (see, e.g., reviews in Bierzychudek 1981; Stephenson 1981; Willson and Burley 1983). Here we offer a simple model showing that natural selection may often act to bring the female's allocation of her reproductive effort to a point where seed production is limited by both pollen supply and provisioning resources. Further, the model indicates that seed production could be expected to respond to a decrease in pollen supply but not to an increase.

Suppose a female allocates an amount a of reproductive effort to attracting pollen and producing immature ovules. The number of ovules that can be fertilized increases with a. Assume further that a is taken from a limited total reproductive effort, such that the number of seeds that the mother can provision to maturity decreases with a (fig. 1). For any given value of a, the number of seeds that can be produced is the lesser of these two functions. The greatest number of seeds can be produced at a^*, where the functions cross. Below a^*, seed production is pollen-limited, and increased allocation to attracting pollen increases seed set. Above a^*, seed production is resource-limited, and reduced allocation to attracting pollen increases the resources available for provisioning seeds. The model illustrates the economic principle that internal resources are optimally allocated among competing processes when each resource limits all processes to the same degree (Bloom et al. 1985). Here we consider only two processes, pollen attraction and ovule provisioning, but the principle would still apply if other processes such as pollen production and vegetative reproduction were included.

The model is best understood on an evolutionary time scale. If seed production of a species is consistently pollen-limited, natural selection should favor individuals that allocate more resources to pollen attraction. If seed production is consistently provisioning-limited, individuals that allocate less to pollen attraction are favored. Of course, the precise position of the two functions will not be the same for all individuals in all years. The allocation to pollen attraction that is selected, a', should give higher seed yields on the average than alternative allocations, but, for a particular individual in a particular year, the functions might intersect to one side or the other of a'. In this sense, the individual could be limited *either* by pollen acquisition *or* by resources available for provisioning.

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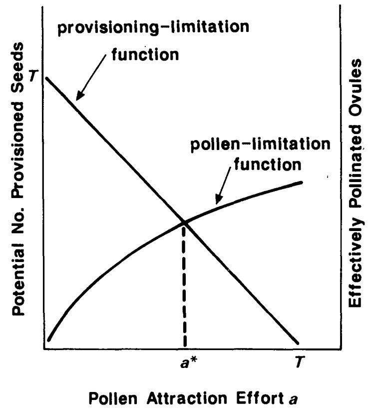

FIG. 1.—As pollen-attraction effort a (expressed in units of potentially provisioned seeds) increases, the number of effectively pollinated ovules increases ("pollination-limitation function") but the number of potentially provisioned seeds decreases ("provisioning-limitation function"). The actual number of seeds that can be produced is given by the minimum of these two functions for any given value of a. For a total maternal reproductive effort of T, the maximum number of seeds can be produced at a^*, where the functions cross. An individual's actual allocation, a' (see the text), would be expected to lie near a^*.

However, if many individuals were considered over many years, one would have to conclude that the species is limited by *both* pollen acquisition and resources.

It is usually assumed that when an input limits an output, increased input leads to increased output and decreased input leads to decreased output. This is not the case at a^*. The classical experiment testing for pollen limitation is the addition of extra pollen followed by observation to see if seed set increases. At a^* this experiment would not increase seed set, but it would be only partially correct to draw the conclusion that pollen was not limiting, because a reduction in pollen supply would produce a decrease in seed set.

Because of the unpredictability of pollen supply, a plant's allocation, a', is unlikely to be precisely a^*. If a' is less than a^*, seed set should respond to additional pollen; but unless a' is far from a^*, this response should be small. Thus, most pollen-addition experiments should fail to cause major increases in seed set. The exceptions should occur in species in which pollen supply is highly variable and a' is significantly less than a^* in some years. Consider what would be expected if pollen reaching stigmas were reduced by a controlled amount. In practice such an experiment would be difficult (total exclusion aside), but thinking about the experiment is useful. For a' less than or equal to a^*, any reduction in pollen should reduce seed set, but for a' greater than a^*, some minimum reduction in pollen is required to reduce seed set. Resource manipulation will not be discussed here except to emphasize that the outcome depends on the timing of manipulation relative to that of allocation. Additional resources could contribute to both provisioning and pollen attraction or to provisioning alone.

A central premise of the model is that both pollen acquisition and seed provisioning have costs to the mother; neither activity can be increased without interfering with some other fitness-affecting activity. This premise is of a type frequently used in evolutionary ecology, but this does not mean that the premise is beyond question. For example, competition among flowers to donate pollen might set pollen supply at such a high level that there is no cost of pollen attraction, or resource use could be organized such that resources used for seed provisioning could not be reallocated to pollen acquisition. Such a restraint on reallocation seems quite likely over ecological time but is harder to accept over evolutionary time. The model also assumes that unused provisioning resources cannot be used at a subsequent reproductive event. The model has many potential complications, which require a more formal analysis than our simple graphic approach. However, as long as pollen attraction and seed provisioning both have costs, there is always an evolutionary option of investing less in pollen attraction to have more resources available for seed provisioning (and vice versa).

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